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LABOULBENIALES ON SEMIAQUATIC HEMIPTERA. IV.
ADDENDA TO *PROLIXANDROMYCES*

Richard K. Benjamin

Abstract.—Three new species of *Prolixandromyces* (Ascomycetes: Laboulbeniales), all parasites on *Velia* (Hemiptera: Veliidae), are described and illustrated: *P. lingulatus*, *P. rhinoceralis*, and *P. tenuis*. A key to the five species presently known is given. The two species described originally, *P. veliae* and *P. corniculatus*, were found in Michoacan in southern Mexico; the range of *P. corniculatus* is extended to El Salvador. *Prolixandromyces lingulatus* and *P. rhinoceralis* were collected in Nicaragua and *P. tenuis* in Costa Rica.

Introduction

In the second of my earlier reports on Laboulbeniales found on semiaquatic Hemiptera (Benjamin 1967, 1970, 1979¹), I described the genus *Prolixandromyces* and compared it to presumably related genera thought to be allied to *Stigmatomyces* Karsten. All species of the genera of this assemblage have a simple receptacle composed of but three superposed cells. The basal cell (I) forms the foot, the organelle of attachment to the host; the suprabasal cell (II) gives rise typically to a single, stalked perithecium; and the terminal cell (III) subtends a few- to many-celled appendage that lacks sterile branchlets and forms one or more simple antheridia. *Prolixandromyces* was distinguished generically because of the extremely oblique superposition of cells I and II of the receptacle and because of the greatly elongated discharge tubes of the two antheridia formed distally on a three-celled appendage. The perithecium of both species described in 1970, *P. veliae* and *P. corniculatus*, parasitic on species of *Velia* Latreille, bears a distinctive hornlike terminal appendage, but this feature was not stressed as a generic characteristic pending discovery of additional species.

In 1973, Dr. John Polhemus, Englewood, Colorado, kindly permitted me to survey his collection of semiaquatic Hemiptera for Laboulbeniales (Benjamin 1979). Among the fungi discovered at this time were three additional species of *Prolixandromyces*, also on bugs of the genus *Velia*. These are herein described and illustrated.

I wish again to express my gratitude to Dr. Polhemus for his aid in furthering my studies of Laboulbeniales. I also thank Dr. Isabelle Tavares for reviewing the manuscript and the National Science Foundation for equipment grant DEB-7812891 to the Rancho Santa Ana Botanic Garden which

provided funds for purchasing a microscope equipped with interference contrast optics. This instrument has been of especial value to me in discerning details of structure and development in Laboulbeniales.

Descriptions and Commentary

Prolixandromyces Benjamin, Aliso 7(2):174. 1970.

Key to the Species

- A. Length of perithecial stalk cell exceeding length of perithecial body 5. *P. tenuis*
 - Stalk cell much shorter than perithecial body B
- B. At least one terminal wall cell of perithecium forming a conspicuous, more or less erect, curved or sinuate, acuminate, hornlike appendage C
 - Perithecium without such an appendage; one terminal wall cell forming only a relatively short, horizontally directed, ligulate outgrowth. *P. lingulatus*
- C. Only one terminal wall cell giving rise to an appendage; the others relatively unmodified distally D
 - All four terminal wall cells forming distal prolongations; one cell forming a conspicuous, divergent, hornlike outgrowth; the others with slender, ligulate terminations 4. *P. rhinoceralis*
- D. Perithecial appendage stout, nearly erect, slightly curved 2. *P. corniculatus*
 - Perithecial appendage somewhat recurved, slightly sinuate 1. *P. veliae*

1. *Prolixandromyces veliae* Benjamin, Aliso 7(2):175, Fig. 4A–E. 1970. Fig. 10

Prolixandromyces veliae, the type species, was described from specimens growing on the femur of the right rear leg of a male of *Velia* sp. collected near Jacona, Michoacan, Mexico, by David Lauck in 1957. Four mature individuals of the same species, one of which is shown in Fig. 10, were found on the trochanter of the right middle leg of a male of a species of *Velia* collected by Dr. Polhemus (CL 1261) in Nicaragua (Rio Tapacales, Dec. 22, 1969; RKB 2862A; slide in RSA). The Nicaraguan specimens differ from the type collection only in being somewhat longer, 475–525 μm vs. 300–440 μm . This difference in dimensions is due to the greater length of the perithecium: stalk cell 120–150 μm vs. 75–120 μm ; perithecial body 280–310 μm vs. 215–275 μm . The ascospores of the type measure ca. 40 $\mu\text{m} \times 5\text{--}6 \mu\text{m}$; those of the Nicaraguan specimens are 40–45 $\mu\text{m} \times 5\text{--}7 \mu\text{m}$. Di-

mensions of the receptacle, appendage, and perithecial appendage in both collections are similar.

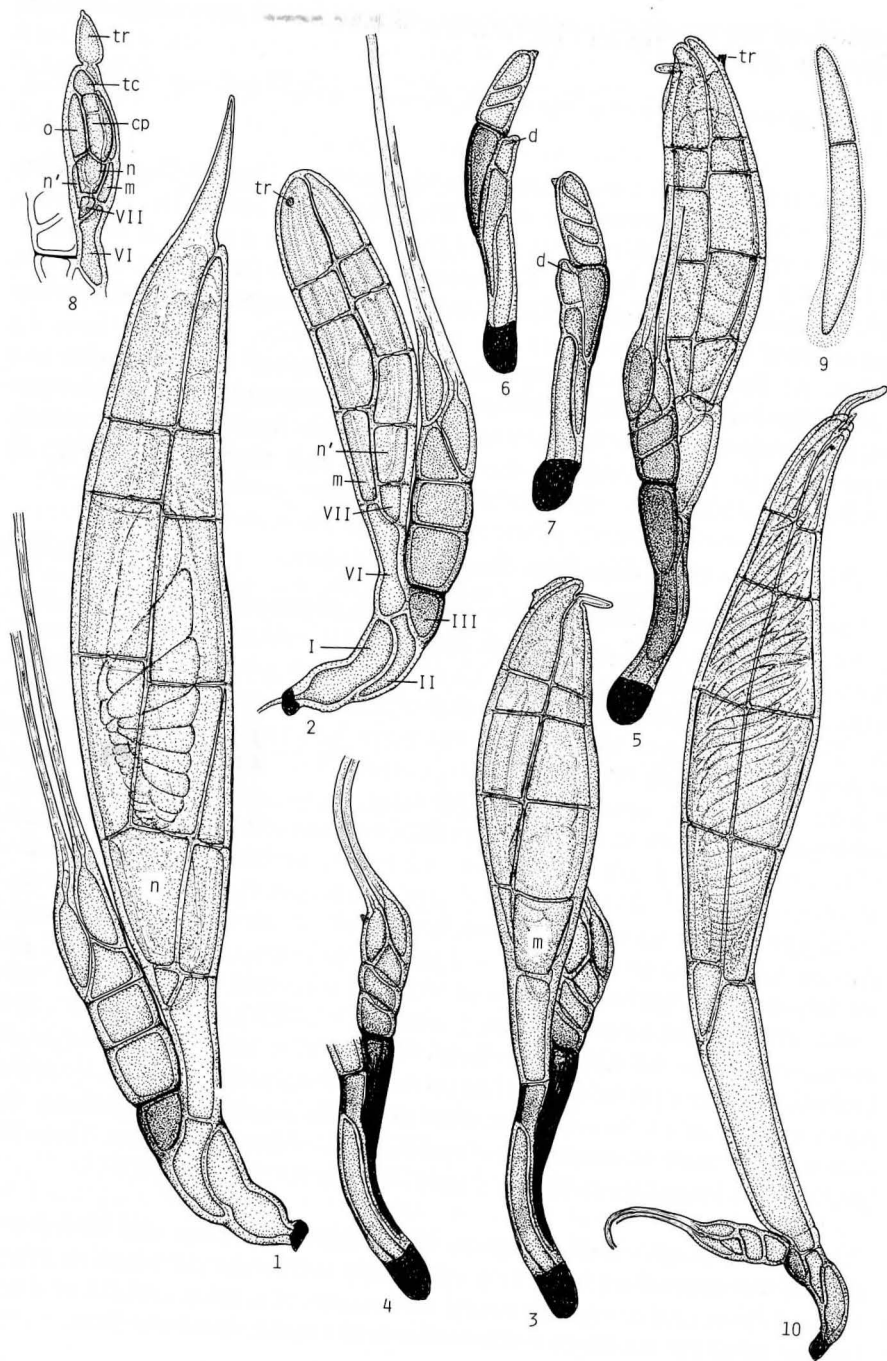
2. *Prolixandromyces corniculatus* Benjamin, Aliso 7(2):177, Fig. 4F–J. 1970. Fig. 1–2

This species, which was described from species of *Velia* collected by Dr. Lauck, was not encountered on any of the insects supplied by Dr. Polhemus. The holotype (*RKB 2073B*) was taken from the lower surface of the mesothorax of a male from Jacona, Michoacan, Mexico, whereas the other two collections reported originally (*RKB 2072, 2074*) were growing on the pronotum of two females, one from the Mexican locality, the other from La Union, El Salvador. I am supplementing my original drawings with two more (Fig. 1–2; from *RKB 2074*) which show early and late stages of perithecial development to be discussed later. These figures more accurately depict cellular relationships in the perithecial wall than does my Fig. 4F published in 1970.

3. *Prolixandromyces lingulatus* Benjamin, sp. nov. Fig. 3–9

Fungus ochraceobubalinus. *Receptaculum* elongatum, rectum vel arcuatum, $50\text{--}60\ \mu\text{m} \times 10\ \mu\text{m}$, marginibus posticis cellularum II et III memnoniis; cellula I elongata, tenuis, $32\text{--}43\ \mu\text{m} \times 5\text{--}6\ \mu\text{m}$; cellula II elongata, tenuis, $25\text{--}30\ \mu\text{m}$ longa, $5\text{--}6\ \mu\text{m}$ in diametro ad apicem; cellula III elongata, $20\text{--}25\ \mu\text{m} \times 5\text{--}7\ \mu\text{m}$ ad apicem, cum parte basi postica stipitis perithecii conjuncta. *Appendix* $60\text{--}80\ \mu\text{m}$ longa; corpus $21\text{--}27\ \mu\text{m} \times 10\text{--}11\ \mu\text{m}$, septo basilari constricto, opaco; cellula basilaris $10\text{--}14\ \mu\text{m} \times 9\text{--}10\ \mu\text{m}$; cellula subbasilaris $6\text{--}7\ \mu\text{m} \times 10\text{--}12\ \mu\text{m}$; cellula superna a latere visa triangularis, $6\text{--}10\ \mu\text{m}$ alta, $7\text{--}9\ \mu\text{m}$ in diametro ad basin; venteres antheridiorum ad apicem conjuncti, $10\text{--}15\ \mu\text{m} \times 5\text{--}6\ \mu\text{m}$; antheridium anticum spiniferum; spina obtusa, fuscata; tubi antheridiorum liberi, elongati, erecti, modice curvati; tubus anticus $30\text{--}45\ \mu\text{m} \times 2\ \mu\text{m}$; tubus posticus $30\text{--}35\ \mu\text{m} \times 2\ \mu\text{m}$. *Perithecium* elongatum, $80\text{--}85\ \mu\text{m} \times 23\text{--}26\ \mu\text{m}$, fere symmetricum, margines prope uniformiter convexae; cellula VI $21\text{--}23\ \mu\text{m}$ longa, $7\text{--}8\ \mu\text{m}$ ad basin, $10\text{--}11\ \mu\text{m}$ ad apicem; cellula VII parva, a latere visa triangularis; cellulae basiliares prope 0.2 perithecii in tota longitudine; cellula terminalis seriei cellulosa ex *m*-cellula basilari oriundae appendicem ligulatam, $6\text{--}7\ \mu\text{m} \times 2\ \mu\text{m}$, faciens. Ascosporae hyalinae, $33\text{--}37\ \mu\text{m} \times 3\text{--}4\ \mu\text{m}$. Totus fungus $157\ \mu\text{m}$ longus (individuum unum). Typus *RKB 2862B* (RSA).

Near Ochraceous-Buff (Ridgway 1912); lower posterior and lateral margins of the appendage becoming externally suffused with blackish brown, the suffusion extending downward and nearly obscuring cell III of the receptacle and the posterior surface of cell II to just above the foot.



Receptacle: Elongate, slender, 50–60 μm by ca. 10 μm in greatest width, straight to arcuate; basal cell (I), including foot, slender, much longer than broad, 32–43 $\mu\text{m} \times 5\text{--}6 \mu\text{m}$; suprabasal cell (II) and basal cell obliquely superposed; cell II slender, 25–35 μm long, broadest distally, 5–7 μm where it subtends the stalk cell (VI) of the perithecium and separates the latter from the distal end of cell I, more or less suffused above with blackish brown; cell III smaller, elongate, 20–25 μm long, broadest above, 5–7 μm wide where it subtends the appendage, its distal, anterior margin and the lower posterior margin of the perithecial stalk cell adnate, extending downward along the posterior margin of cell II well beyond the level of the distal end of cell I.

Appendage: Body consisting of three superposed, slightly rounded cells separated from one another by oblique cross walls, 21–27 μm to tip of upper cell by 10–11 μm ; basal cell 10–14 $\mu\text{m} \times 9\text{--}10 \mu\text{m}$, the anterior margin ca.

←

Figs. 1–10.—1–2. *Prolixandromyces corniculatus*.—1. Immature individual in late stages of development showing the prominent, hornlike appendage that has arisen from the terminal cell of the posterolateral row of outer wall cells derived from basal cell *n*. Spiraling of the perithecium and displacement of the basal cells have altered the position of the wall-cell rows from their earlier, nearly vertical alignment as shown in Fig. 2. $\times 690$.—2. Immature individual showing relationship of young perithecium to the receptacle and appendage. Above the stalk cell (VI), the secondary stalk cell (VII) is in a posterior position facing the appendage. Basal cell *m* is positioned more or less anterolaterally; basal cell *n'* is positioned posterolaterally. Each of these cells has given rise to a single vertical row of wall cells. The row derived from *m* still consists of only three cells and bears the trichogynic remnant (*tr*) distally, whereas the row derived from *n'* consists of four cells. Basal cell *n* lies on the opposite side of the perithecium and has given rise to one posterolateral and one anterolateral row of outer wall cells, each consisting of four cells. $\times 620$.—3–9. *Prolixandromyces lingulatus*.—3. Anterolateral view of the mature type showing the laterally directed ligulate appendage terminating the upper cell of the wall-cell row derived from basal cell *m*. Note spiraling of perithecium. $\times 620$.—4. Receptacle and appendage of type specimen shown in Fig. 3. Note receptacular pigmentation and spinose remnant of spore apex on body of anterior antheridium. $\times 620$.—5. Posterolateral view of nearly mature individual showing trichogynic remnant (*tr*) on upper cell of posterolateral row of wall cells derived from basal cell *n*. $\times 620$.—6–7. Two immature individuals showing early stages of development of the appendage. The distal cell of the appendage shown in Fig. 6 has divided once in the appendage shown in Fig. 7. The upper cell will give rise to the terminal, posterior antheridium shown in Fig. 4; the subterminal cell will divide again and form cell three of the mature appendage and the anterior antheridium bearing the spore-tip remnant as shown in Fig. 4. The primordial cell of the perithecium and procarp (*d*) has been cut off distally from the subbasal cell of the receptacle. $\times 620$.—8. Perithecium in early stage of development showing the stalk cell (VI); secondary stalk cell (VII); the three basal cells (*m*, *n*, and *n'*); the first wall cells (*o*); and the carpogenic upgrowth consisting of the carpogenic cell (*cp*), trichophoric cell (*tc*), and trichogyne (*tr*). The relationship of the perithecium to the receptacle and appendage, both of which are mature at this stage of development, is shown. $\times 690$.—9. Ascospore. $\times 1100$.—*Prolixandromyces veliae*. One of four mature individuals from the Nicaraguan collection (RKB 2862A). $\times 250$.

two times the height of the posterior margin, slightly constricted below where separated from cell III of the receptacle by a transverse, externally opaque cross wall; suprabasal cell about half as high as wide, $6-7\ \mu\text{m} \times 10-12\ \mu\text{m}$, the opposite walls more or less parallel in lateral view; terminal cell triangular in lateral view, $6-10\ \mu\text{m}$ high by $7-9\ \mu\text{m}$ wide at the base, its lower posterior margin free and slightly convex, its upper posterior and anterior walls united with the antheridial venters, which are united above the apex of the terminal cell; venters $10-15\ \mu\text{m} \times 5-6\ \mu\text{m}$; venter of the anterior antheridium bearing a prominent, blunt, darkened spinose projection; antheridial discharge tubes free, moderately curved, elongate; anterior tube $30-45\ \mu\text{m} \times 2\ \mu\text{m}$; posterior tube $30-35\ \mu\text{m} \times 2\ \mu\text{m}$. Total length to tip of longest antheridial discharge tube $60-80\ \mu\text{m}$.

Perithecium: Stalk cell (VI) $21-23\ \mu\text{m}$ long, $7-8\ \mu\text{m}$ wide at the base, $10-11\ \mu\text{m}$ wide below the basal cells; secondary stalk cell (VII) small, triangular in lateral view; basal cells (*m*, *n*, *n'*) constituting ca. 20% of the total length of the perithecial body; body of perithecium nearly straight, broadest near the middle, $80-85\ \mu\text{m} \times 23-26\ \mu\text{m}$, tapered to a bluntly rounded apex; the terminal cell of the row of wall cells derived from basal cell *m* bearing distally a laterally directed, ligulate appendage $6-7\ \mu\text{m} \times 2\ \mu\text{m}$; the terminal cells of the other rows of wall cells each forming a terminal, rounded umbo; the darkened remnant of the base of the trichogyne borne subterminally on the terminal cell of the posterolateral row of wall cells derived from basal cell *n*. Ascospores hyaline, $33-37\ \mu\text{m} \times 3-4\ \mu\text{m}$.

Total length from base of foot to tip of perithecium $157\ \mu\text{m}$ (one mature individual).

Etymology.—From *lingulatus* (L.), tongue-shaped; alluding to the perithecial appendage.

Holotype.—NICARAGUA: Rio Tapacales, Dec. 22, 1969, J. T. Polhemus (CL 1261). On the lower surface of the femur of the left anterior leg of a male of *Velia* sp. (Hemiptera: Veliidae); RKB 2862B (Fig. 3); slide in RSA.

Other specimens examined.—On the legs of other male and female specimens of the same host species from the type locality; RKB 2863A, 2864B, C; slides in RSA.

Single mature and nearly mature individuals (Fig. 3, 5) together with several immature specimens (Fig. 6-8) of *P. lingulatus* have been studied. Maturity of the specimen shown in Fig. 3 is suggested inasmuch as the perithecium contained mature ascospores (Fig. 9) at the time of collection. This species of *Prolixandromyces* differs in one important aspect from the other four found thus far in lacking a prominent spinelike or hornlike perithecial appendage. Instead, the terminal cell of the row of outer wall cells derived from basal cell *m* forms a small, ligulate appendage apically that projects laterally immediately below the perithecial tip (Fig. 3, 5). The stat-

ure of *P. lingulatus* is only one half to one third that of the other species. It is further distinguished by the conspicuous dark pigmentation of the receptacle which nearly obscures cell III and the posterior margin of cell II (Fig. 3, 4). The indurated tip of the original spore often remains as a small, spinose process borne on the upper surface of the anterior antheridium (Fig. 4). Of the other species, a spinose antheridium has been observed only in *P. tenuis* (Fig. 17).

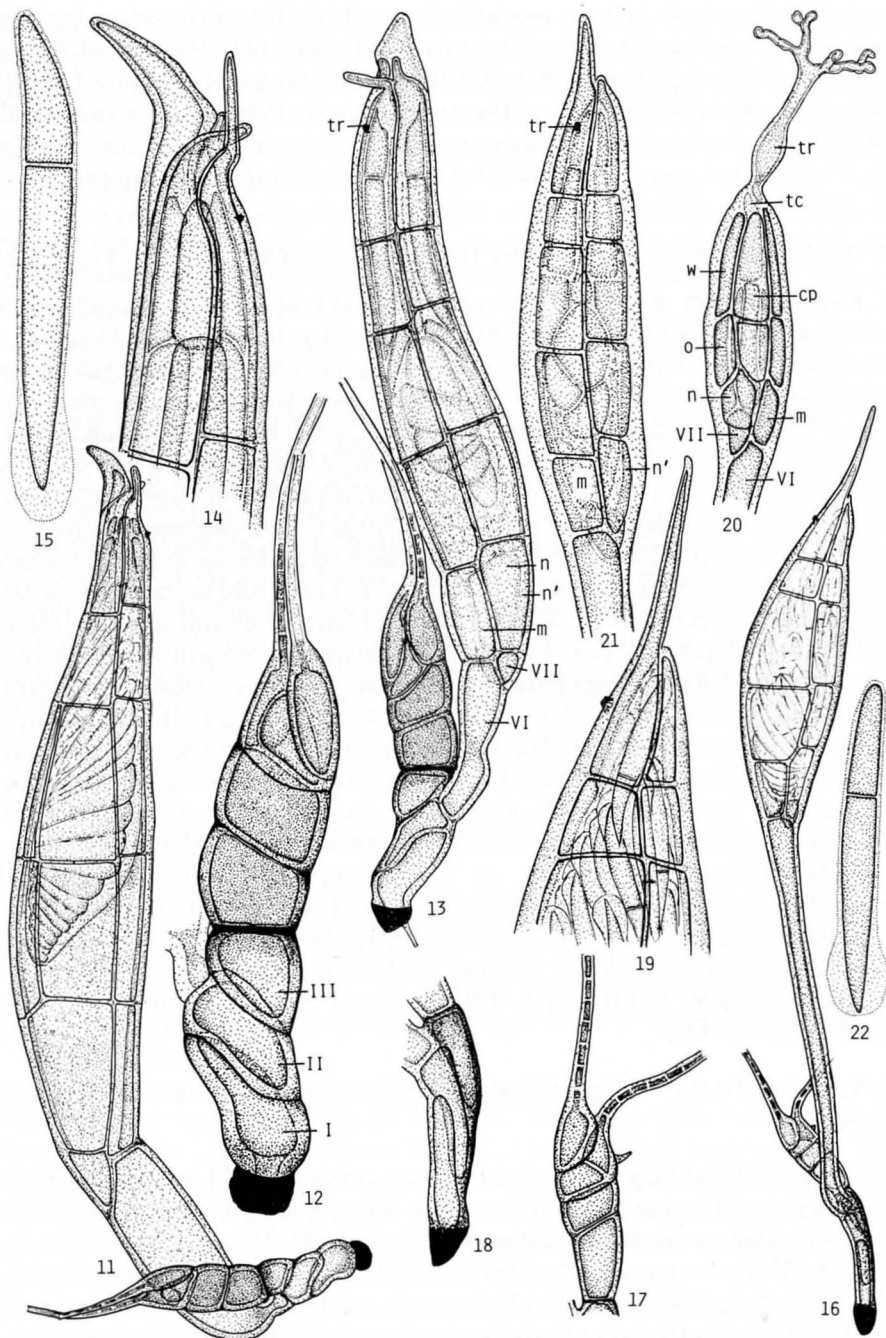
4. *Prolixandromyces rhinoceralis* Benjamin, sp. nov.

Fig. 11–15

Fungus dilutus aurantioflavus; appendix cum brunnea tincta. *Receptaculum* crassum, plus minusve curvatum, $43\text{--}53\ \mu\text{m} \times 20\text{--}23\ \mu\text{m}$; cellula I $30\text{--}35\ \mu\text{m} \times 15\text{--}16\ \mu\text{m}$; cellula II ca. $20\text{--}25\ \mu\text{m}$ longa, $15\text{--}18\ \mu\text{m}$ in diametro ad apicem; cellula III a latere visa plus minusve triangularis, postice convexa, $15\text{--}17\ \mu\text{m}$ longa, $13\text{--}18\ \mu\text{m}$ ad apicem, parte basi postica stipitis perithecii conjuncta. *Appendix* $110\text{--}123\ \mu\text{m}$ longa; corpus $40\text{--}48\ \mu\text{m} \times 21\text{--}22\ \mu\text{m}$; cellula basilaris $15\text{--}20\ \mu\text{m} \times 17\text{--}21\ \mu\text{m}$, septo basilari constricto, opaco; cellula subbasilaris $12\text{--}17\ \mu\text{m} \times 18\text{--}22\ \mu\text{m}$; cellula superna a latere visa triangularis, $15\ \mu\text{m}$ longa, $15\text{--}18\ \mu\text{m}$ in diametro ad basin; venteres antheridiorum ad apicem conjuncti, $18\text{--}23\ \mu\text{m} \times 7\text{--}9\ \mu\text{m}$; tubi antheridiorum liberi, elongati, erecti, leniter curvati; tubus anticus $55\text{--}65\ \mu\text{m} \times 2\ \mu\text{m}$; tubus posticus $40\text{--}50\ \mu\text{m} \times 2\ \mu\text{m}$. *Perithecium* elongatum, $305\ \mu\text{m} \times 62\ \mu\text{m}$, rectum vel sinuolatum, marginibus plus minusve convexis; cellula VI robusta, $118\ \mu\text{m} \times 37\ \mu\text{m}$, basi fortiter et abrupte constricta; cellula VII parva, a latere visa triangularis; cellulae basiliares prope 0.25 perithecii in tota longitudine; cellula terminalis seriei cellulosae ex *m*-cellula basilari oriundae appendicem ligulatam, ca. $20\ \mu\text{m} \times 2\ \mu\text{m}$, faciens; cellula terminalis seriei cellulosae anterolateralis ex *n*-cellula basilari oriundae appendicem robustam, divergentem, acuminatam, ca. $25\ \mu\text{m}$ longam, $12\ \mu\text{m}$ in diametro ad basin, faciens; cellulae terminales serierum cellulosarum posterolateralium et anterolateralium ex *n*- et *n'*-cellulis basilariibus oriundarum appendices singulas ligulatas, ca. $10\ \mu\text{m} \times 2\ \mu\text{m}$, facientes. Ascosporae hyalinae, $52\text{--}60\ \mu\text{m} \times 5\text{--}6\ \mu\text{m}$. Totus fungus $470\ \mu\text{m}$ longus (individuum unum). Typus RKB 2864A (RSA).

Near Pale Orange-Yellow (Ridgway 1912); appendage darker, tinged with brown.

Receptacle: Relatively stout, more or less curved, $43\text{--}53\ \mu\text{m} \times 20\text{--}23\ \mu\text{m}$ in greatest width; basal cell (I) more or less abruptly enlarged above the foot, especially posteriorly, longer than broad, $30\text{--}35\ \mu\text{m} \times 15\text{--}16\ \mu\text{m}$ including the foot; suprabasal cell (II) ca. $20\text{--}25\ \mu\text{m}$ long, broadest distally, $15\text{--}18\ \mu\text{m}$ wide where it subtends the stalk cell (VI) of the perithecium and slightly separates the latter from the distal end of cell I; cell III more or less



triangular in lateral view, rounded posteriorly, 15–17 μm in greatest length, 13–18 μm wide where it subtends the appendage, its distal anterior margin and the lower posterior margin of the perithecial stalk cell adnate, extending downward along the posterior margin of cell II about to the level of the distal end of cell I.

Appendage: Body consisting of three superposed, slightly rounded cells separated from one another by somewhat oblique cross walls, 40–48 μm to tip of upper cell by 21–22 μm ; basal cell 15–20 $\mu\text{m} \times 17$ –21 μm , constricted where separated from cell III of the receptacle by a transverse, externally opaque cross wall; suprabasal cell about as long as broad, 12–17 $\mu\text{m} \times 18$ –22 μm , opposite walls nearly parallel in lateral view; terminal cell triangular in lateral view, 15 μm long, 15–18 μm wide at the base, its posterior and anterior lateral walls united with the antheridial venters; venters of antheridia united above the apex of the terminal cell, 18–23 $\mu\text{m} \times 7$ –9 μm ; antheridial

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Figs. 11–22.—11–15. *Prolixandromyces rhinoceralis*.—11. The mature type (RKB 2864A). $\times 285$.—12. Receptacle and appendage of the type specimen shown in Fig. 11. $\times 690$.—13. Immature individual (RKB 2865) in lateral view showing relationship of the perithecium to the receptacle and appendage. Above the stalk cell (VI), the secondary stalk cell (VII) is in an anterior position facing away from the appendage. Basal cell *m* is positioned more or less posterolaterally and has given rise to a posterolateral row of outer wall cells the upper cell of which is terminated by a ligulate appendage similar to that on the corresponding cell of *P. lingulatus*. This cell also bears the trichogynic remnant (*tr*). Basal cell *n'* has given rise to an anterolateral row of outer wall cells the upper cell of which bears a terminal ligulate appendage somewhat shorter than that terminating the *m* row of wall cells. Basal cell *n* is positioned on the opposite side of the perithecium and has given rise to two rows of outer wall cells. The upper cell of the anterolateral row derived from *n* is forming the conspicuous hornlike appendage shown in Fig. 11 and 14. The upper cell of the posterolateral row of wall cells derived from cell *n* is terminated by a short, ligulate appendage like that terminating the *n'* row of wall cells. $\times 450$.—14. Perithecial apex of a nearly mature individual (RKB 2865) showing the hornlike and ligulate appendages formed by the distal outer wall cells. $\times 690$.—15. Ascospore. $\times 1100$.—16–22. *Prolixandromyces tenuis*.—16. The mature type (RKB 2861). $\times 355$.—17. Appendage of the type specimen showing spinose remnant of the spore apex on the body of the posterior antheridium. $\times 690$.—18. Mature receptacle of another individual from the type collection. $\times 690$.—19. Terminus of the perithecium of the type shown in Fig. 16. Note the elongate, acuminate appendage and trichogynic remnant (*tr*) borne on the same cell. $\times 690$.—20. Perithecium in early stage of development in nearly lateral view showing the stalk cell (VI); secondary stalk cell (VII), which is positioned posteriorly with respect to the appendage (not shown); two of the three basal cells (*m* and *n*); the first two cells of three of the outer rows of wall cells (*o* and *w*) derived from cells *m* and *n*; and the carpogenic upgrowth consisting of the carpogenic cell (*cp*), trichophoric cell (*tc*), and terminally branched trichogyne (*tr*). $\times 690$.—21. Immature perithecium at later stage of development in posterolateral view. The basal cells, only two of which (*m* and *n'*) are depicted in the drawing, have given rise to nearly vertical rows of outer wall cells consisting of four cells each. The terminal cell of the row of wall cells derived from basal cell *m* is forming the perithecial appendage and bears the trichogynic remnant (*tr*). $\times 690$.

5. *Prolixandromyces tenuis* Benjamin, sp. nov.

Fig. 16–22

Fungus aurantiobubalinus. *Receptaculum* elongatum, tenue, $46\text{--}55\ \mu\text{m} \times 8\text{--}10\ \mu\text{m}$; cellula I tenuis, $30\text{--}37\ \mu\text{m} \times 5\text{--}6\ \mu\text{m}$; cellula II tenuis, $25\text{--}32\ \mu\text{m}$ longa, $5\text{--}6\ \mu\text{m}$ in diametro ad apicem; cellula III $18\text{--}22\ \mu\text{m}$ longa, $10\text{--}11\ \mu\text{m}$ in diametro ad apicem, margine postico memnonio, cum parte basi postica stipitis perithecii conjuncta. *Appendix* $62\text{--}67\ \mu\text{m}$ longa; corpus $25\text{--}30\ \mu\text{m} \times 11\text{--}12\ \mu\text{m}$; cellula basilaris $15\text{--}17\ \mu\text{m} \times 10\text{--}11\ \mu\text{m}$, septo basilaris vix constricto, nonopaco; cellula subbasilaris $6\text{--}7\ \mu\text{m} \times 10\text{--}12\ \mu\text{m}$; cellula superna a latere visa plus minusve triangularis ad apicem, margine postico inferno, libero, leniter convexo; venteres antheridiorum ad apicem conjuncti, $8\text{--}12\ \mu\text{m} \times 6\text{--}8\ \mu\text{m}$; antheridium posticum spiniferum; spina ca. $3\ \mu\text{m}$ longa; tubi antheridiorum liberi, elongati; tubus anticus fere erectus, $26\text{--}30\ \mu\text{m} \times 2\ \mu\text{m}$; tubus posticus divergens, sinuolatus, $20\text{--}26\ \mu\text{m} \times 2\ \mu\text{m}$. *Perithecium* elongatum, $114\text{--}122\ \mu\text{m} \times 37\text{--}40\ \mu\text{m}$, prope symmetricum, marginibus convexis; cellula VI elongata, tenuis, $135\text{--}157\ \mu\text{m} \times 7\text{--}8\ \mu\text{m}$, $12\text{--}13\ \mu\text{m}$ ad apicem; cellula VII parva, a latere visa triangularis; cellulae basiliares prope 0.15 perithecii in tota longitudine; cellula terminalis seriei cellulosa ex *m*-cellula basilari oriundae appendicem tenuem, erectam, acuminatam, ca. $35\ \mu\text{m}$ longam, faciens. Ascosporae hyalinae, $38\text{--}42\ \mu\text{m} \times 4\text{--}5\ \mu\text{m}$. Totus fungus $312\text{--}345\ \mu\text{m}$ longus (individua tria). Typus RKB 2861 (RSA).

Near Orange-Buff (Ridgway 1912); posterior margin of receptacle, especially cell III, tinged blackish brown.

Receptacle: Elongate, slender, $46\text{--}55\ \mu\text{m}$ long by $8\text{--}10\ \mu\text{m}$ in greatest width, slightly curved, basal cell (I), including the foot, slender, several times longer than broad, $30\text{--}37\ \mu\text{m} \times 5\text{--}6\ \mu\text{m}$; suprabasal cell (II) and basal cell obliquely superposed; cell II slender, $25\text{--}32\ \mu\text{m}$ long, broadest distally, $5\text{--}6\ \mu\text{m}$ wide where it subtends the stalk cell (VI) of the perithecium and separates the latter from the distal end of cell I; cell III smaller, $18\text{--}22\ \mu\text{m}$ long, broadest above, $10\text{--}11\ \mu\text{m}$ wide where it subtends the appendage, its distal anterior margin and the lower posterior margin of the perithecial stalk cell adnate, extending downward along the posterior margin of cell II well beyond the level of the distal end of cell I.

Appendage: Body consisting of three superposed, slightly rounded cells separated from one another by more or less oblique cross walls, $25\text{--}30\ \mu\text{m}$ to tip of upper cell by $11\text{--}12\ \mu\text{m}$; basal cell $15\text{--}17\ \mu\text{m} \times 10\text{--}11\ \mu\text{m}$, widest above, slightly constricted below where separated from cell III of the receptacle by a transverse cross wall; suprabasal cell about half as long as broad, $6\text{--}7\ \mu\text{m} \times 10\text{--}12\ \mu\text{m}$, the opposite walls nearly parallel in lateral view; terminal cell more or less triangular above in lateral view, its lower posterior margin free and slightly convex; its upper posterior and anterior

lateral walls united with the antheridial venters; venters of antheridia united above the apex of the terminal cell, $8\text{--}12\text{ }\mu\text{m} \times 6\text{--}8\text{ }\mu\text{m}$; venter of posterior antheridium bearing a prominent, acuminate spine ca. $3\text{ }\mu\text{m}$ long; antheridial discharge tubes free, elongate; anterior tube nearly erect, $26\text{--}30\text{ }\mu\text{m} \times 2\text{ }\mu\text{m}$; posterior tube divergent, slightly sinuate, $20\text{--}26\text{ }\mu\text{m} \times 2\text{ }\mu\text{m}$. Total length to tip of longest antheridial discharge tube $62\text{--}67\text{ }\mu\text{m}$.

Perithecium: Stalk cell (VI) slender, elongate, $135\text{--}157\text{ }\mu\text{m} \times 7\text{--}8\text{ }\mu\text{m}$, widening distally to $12\text{--}13\text{ }\mu\text{m}$ below the perithecial base; secondary stalk cell (VII) small, triangular in lateral view; basal cells (*m*, *n*, *n'*) constituting ca. 15% of the total length of the perithecial body, excluding the terminal appendage; body of perithecium elongate, $114\text{--}122\text{ }\mu\text{m} \times 37\text{--}40\text{ }\mu\text{m}$ including the basal cells, nearly symmetrical, broadest near the middle, tapered gradually to the narrowly rounded apex; the terminal cell of the outer wall-cell row derived from basal cell *m* bearing externally below the tip the darkened remnant of the trichogynic base and forming terminally a slender, erect, acuminate appendage ca. $35\text{ }\mu\text{m}$ long. Ascospores hyaline, $38\text{--}42\text{ }\mu\text{m} \times 4\text{--}5\text{ }\mu\text{m}$.

Total length from base of foot to tip of perithecial appendage $312\text{--}345\text{ }\mu\text{m}$ (three mature individuals).

Etymology.—From *tenuis* (L.), slender; alluding to the habit of the thallus, especially the perithecial stalk cell.

Holotype.—COSTA RICA: 10 mi S of Palmar Sur, Dec. 28, 1969, J. T. Polhemus (CL 1281). On lower surface of femur of right rear leg of male of *Velia virtutis* Drake & Harris (Hemiptera: Veliidae); RKB 2861 (Fig. 16); slide in RSA.

The only collection of *P. tenuis* available for study consists of three mature individuals including the type (Fig. 16, 17, 19); two immature specimens, the developing perithecia of which are shown in Fig. 20, 21; and eight mature receptacles with only their associated appendages intact. The species is readily distinguished from the other members of the genus by its perithecial stalk cell which is considerably longer than the body of the perithecium proper including the basal cells (Fig. 16). Unlike *P. veliae*, *P. corniculatus*, and *P. rhinoceralis*, in which the hornlike perithecial appendage arises from one of the two rows of outer wall cells derived from basal cell *n*, the elongate, acuminate appendage of *P. tenuis* arises terminally from the row of wall cells derived from basal cell *m*. In this regard, it resembles *P. lingulatus* in that the ligulate cell of this species also terminates the row of outer wall cells derived from basal cell *m*. As in *P. lingulatus*, one of the antheridia of *P. tenuis* bears a prominent spine (Fig. 17). However, the spine in *P. tenuis* is borne on the posterior antheridium rather than on the anterior antheridium as in *P. lingulatus* (Fig. 4).

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Discussion

With the addition of three species to the two already known, the status of *Prolixandromyces* as a valid taxon seems secure. The genus was distinguished originally from other presumably related genera (tribe Stigmatomyceteae sensu Thaxter 1908) on the basis of the receptacle and appendage (Benjamin 1970). In the discussion of thalloid parts to follow, the terms posterior and anterior refer to the relationship of the perithecium and appendage to one another, i.e., the anterior margin of the appendage faces the posterior margin of the perithecium.

Receptacle: The extreme oblique superposition of cells I and II remains as one of the primary characteristics distinguishing *Prolixandromyces* from other genera of the Stigmatomyceteae with only a few exceptions as noted earlier (Benjamin 1970: p. 181). In *P. veliae*, *P. corniculatus*, and *P. rhinoceralis* the distal extremity of cell I may approach or even contact the lower, anterior surface of the perithecial stalk cell, but in *P. lingulatus* and *P. tenuis* the distal part of cell II usually keeps these cells well separated. Otherwise, variability in the receptacle of all species of *Prolixandromyces* involves only cellular dimensions and pigmentation.

Appendage: Characteristics of the mature appendage of *P. rhinoceralis*, *P. lingulatus*, and *P. tenuis* are the same as for those described originally for *P. veliae* and *P. corniculatus* (Benjamin 1970). The body consists of three superposed cells surmounted by a pair of partially adnate antheridia that form extremely elongate discharge tubes. Only in *P. lingulatus* were immature specimens found that allow one to deduce the course of development of the appendage from the upper segment of the spore (Fig. 6, 7). The receptacle, derived from the lower segment of the spore, reaches nearly mature dimensions very early in development, and by the time cell II has cut off distally the cell from which the perithecium will arise (Fig. 6d, 7d), the incipient appendage has been divided into three, then four superposed cells (Fig. 6, 7). From examination of the mature appendage (Fig. 4), it can be inferred that the terminal cell of the four cells shown in Fig. 7 develops directly into the upper, posterior antheridium and that the subterminal cell divides once and forms the anterior antheridium and cell three of the body of the appendage. In *P. lingulatus* the indurated apex of the spore (Fig. 6, 7) remains as a small spinose protuberance on the anterior antheridium (Fig. 4). Based on the relationship of the antheridia and cell three of the appendage, one may conclude that development of the appendages of *P. veliae*, *P. corniculatus*, and *P. rhinoceralis* follows a similar course, i.e., the upper antheridium is posterior and the lower antheridium, derived from cell three

of the appendage, is anterior. In none of the latter three species has a spine been detected on one of the antheridia.

Development of the appendage in *P. tenuis* is similar to that observed in the other four species, based on its structure when mature, but the position of the antheridia is reversed. The upper antheridium is anterior and the lower antheridium, which bears a conspicuous spine, is posterior (Fig. 17). Although borne on opposite sides of the appendage, the spine-bearing antheridium of *P. lingulatus* and *P. tenuis* has the same origin, i.e., they are derived from cell three of the young appendage. Interspecific variation in antheridial orientation, whether anteriorly or posteriorly directed, is common in the large genus *Stigmatomyces* (Thaxter 1908, 1931) and this feature has taxonomic significance only at the species level.

Perithecium: Perithecial development in *Prolixandromyces* is of the so-called "normal type" described many years ago by Thaxter (1896) for *Laboulbenia* Montagne & Robin and *Stigmatomyces* and subsequently for many other genera. Perithecia of this type originate directly from intercalary cells of the receptacle or from a branch arising from the receptacle. In 1970 Tavares adopted a system of numbering and lettering the cells of the receptacle and perithecium based on an earlier modification by Benjamin and Shanor (1950) of Thaxter's system, and her nomenclature is to be preferred over those of earlier authors (for additional details see Tavares 1973, 1980; Tavares and Majewski 1976). All Laboulbeniales except *Herpomyces* Thaxter have "normal" perithecial development in which a stalk cell (cell VI) and a secondary stalk cell (Cell VII) give rise to three basal cells (Cells *m*, *n*, and *n'*). The basal cells, in turn, give rise to four vertical rows of inner and outer wall cells: one row of each from cell *m*; one row of each from cell *n'*; and two rows of each from cell *n*. The wall-cell rows grow upward and envelop the carpogonial upgrowth, or female sexual structure, *after* it has begun to develop. Tavares (1977, 1980) proposes classifying the Laboulbeniales into two suborders based on perithecial development. Those taxa having normal-type development are to be placed in suborder Laboulbeniineae, whereas *Herpomyces*, in which the perithecial wall begins to develop *before* the formation of the carpogonial upgrowth, is to be placed in suborder Herpomycetinae (Tavares 1981).

In *Prolixandromyces* the fertile branch begins as a cell cut off distally from cell II of the receptacle (Fig. 6d, 7d). From studies of other genera having the same type of perithecial development (*Balazucia* Benjamin [1968]; *Botryandromyces* Tavares & Majewski [1976]; *Filariomyces* Shanor [1952]; *Laboulbenia* [Thaxter 1896]; *Peyritsiella* Thaxter [1896]; *Rhizopodomycetes* Thaxter [Benjamin 1979]; *Stigmatomyces* [Dainat 1973; Thaxter 1896]) it is known that the fertile branch divides into two cells, the upper being the procarp primordium and the lower being the perithecial primor-

dium. Progeny of the upper cell form the female sexual apparatus: the basal carpogenic cell (*cp*); the subbasal trichophoric cell (*tc*); and the terminal trichogyne (*tr*) (Fig. 8, 20). Progeny of the lower cell form the perithecium, the walls of which envelop the developing carpogonial upgrowth and finally the asci and ascospores (Fig. 1-3, 8, 10, 11, 13, 16, 20, 21).

Each vertical row of outer wall cells in the species of *Prolixandromyces* studied consists of four cells, and I have found no evidence of further division of any of the terminal cells.

Immature perithecia bearing intact trichogynes have been found in only two species of *Prolixandromyces*. In *P. lingulatus* the single trichogyne observed consists of a small, single-celled, acuminate, basally rounded upgrowth (Fig. 8). At the stage of perithecial development shown in the figure, the appendage, only part of which is indicated, is fully mature. As the perithecium matures, a darkened remnant of the trichogynal base is displaced downward and forms a small protuberance on the terminal cell of the posterolateral row of outer wall cells derived from basal cell *n*. In *P. tenuis* the single trichogyne observed also is single celled; however, it is several times longer than broad, has a swollen base, and forms several slender branchlets terminally (Fig. 20). In mature specimens of this species, and in *P. veliae*, *P. corniculatus*, and *P. rhinoceralis* as well, the displaced trichogynic remnant occurs on the terminal cell of the row of outer wall cells derived from basal cell *m*. Position of the trichogynal remnant on the mature perithecium of a given species appears to be constant.

The secondary stalk cell (VII) of all species of *Prolixandromyces* is relatively small and inconspicuous compared to the often elongate stalk cell (VI) and the three basal cells; the latter cells may constitute from 15% to 25% or more of the total length of the perithecial body (Fig. 1, 3, 10, 11, 16; Benjamin 1970, Fig. 4A, F). In four species, *P. veliae*, *P. corniculatus*, *P. lingulatus*, and *P. tenuis*, cell VII is in a posterior position in the perithecium below the basal cells where it faces the appendage (Fig. 1, 2, 5, 8, 10, 16). Only in *P. rhinoceralis* does cell VII face the anterior margin of the perithecium (Fig. 11, 13) as is usually the case in other related genera. As a result, the position of cells *m*, *n*, and *n'* and the wall-cell rows derived from them are reversed in *P. rhinoceralis* relative to their position in the other species. The lower end of basal cell *m* always abuts directly against the upper end of cell VI. Cell VII is separated from cell VI by an oblique septum, and basal cells *n* and *n'* are positioned laterally above it where they, along with cell *m*, eventually form the lower part of the perithecial cavity (Fig. 3, 5, 10, 11, 16).

The four vertical rows of outer wall cells derived from the three basal cells are oriented postero- and anterolaterally during early stages of development (Fig. 2, 13, 21). With maturation, the perithecium of some species may undergo a degree of spiraling which displaces the distal cells of each

row away from vertical relative to the proximal cells (Fig. 3). Thus, the perithecial appendage on the immature perithecium of *P. corniculatus* projects upward from a posterolateral position (Fig. 1), whereas in fully mature individuals the appendage always projects upward from an anterolateral position (Benjamin 1970, Fig. 4F).

In answer to a question I posed in 1970, discovery of one species of *Prolixandromyces*, *P. lingulatus*, that lacks a distinctive hornlike perithecial appendage negates the value of such an appendage as a generic characteristic. A further indication that such appendages in this genus have taxonomic significance only at the species level is a difference in their origin from cells of the perithecial apex. The long, spinose protuberance of the perithecium of *P. tenuis* (Fig. 16) arises from the terminal cell of the row of outer wall cells derived from basal cell *m* (Fig. 16, 21). The terminal cell of the *m* row of wall cells in both *P. lingulatus* and *P. rhinoceralis* also produces an upgrowth, but it remains relatively unmodified (Fig. 3, 13, 14) compared to the spinose protuberance of *P. tenuis* and the prominent appendages of the other species. The sturdy appendage of *P. veliae* (Fig. 10) and the hornlike appendages of *P. corniculatus* (Fig. 1) and *P. rhinoceralis* (Fig. 11, 13, 14) arise in each case from the terminal cell of one of the *n*-derived rows of outer wall cells. Only in *P. rhinoceralis* does the terminal cell of the wall-cell row derived from basal cell *n'* produce a ligulate outgrowth as does its opposite neighbor terminating the other row of wall cells derived from basal cell *n* (Fig. 13, 14). One can speculate that the perithecial appendages of these species are in some way involved in spore dispersal, but elucidation of such involvement, if any, on the basis of the kinds of observations presented here is not possible.

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Footnote

¹ Please correct the following orthographic error in my earlier paper on *Rhizopodomyces* (Benjamin 1979); the epithet *polhemusii* should read *polhemi*.